Effects of canopy size on the stratification and shade adaptation of zooxanthallae and chlorophyll in the reef coral *Pocillopora damicornis*

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Abstract

The distribution of chlorophyll in the upper and lower canopy of the coral *Pocillopora damicornis* was measured. Chlorophyll concentration per unit tissue area and per cell is higher in the lower canopy. The data were compared to the chlorophyll concentrations gathered at the blue water Station Aloha 100 km north of the island of Oahu. Integrated concentrations of chlorophyll on the coral reef per m2 is substantially higher than the integrated water column chlorophyll concentration for the deep water station. This implies the reef flat to be more productive per unit area than the open ocean.

Introduction

Pocillopora damicornis is found mainly on subtidal reefs and flourishes in areas of moderate water motion. It is highly phototrophic and symmetrical, with evenly spaced branches and a well developed canopy. This structure of the corallum appears to produce an optimal hydrodynamic environment for the polyps as well as their symbiotically contained dinoflagellate algae. (Chamberlain and Graus, 1975; Jokiel, 1978). The canopy of the corallum optimizes self-shading and thereby enhances harvesting of available Photosynthetic Active Radiation (PAR) for the contained zooxanthallae. Irradiance diminishes within the canopy structure. Structural limitations impose the need for shade adaptation. For example, under low levels of irradiation, zooxanthallae photoadapt by increasing photosynthetic pigmentation content and by modifying photosynthetic response.(Chang et al., 1983) Chlorophyll distribution is very stratified in the coral. The tissues of the branch tips are transparent, yet the the color gradually mutates to brown, deep within the corallum. Shade adaptation involves increases in chlorophyll concentrations along with many other metabolic changes not addressed in this paper. The response of the corallum is therefore the sum of the responses of many "layers", each with its own irradiance capacity and cells in different states of photoadaptation (Jokiel and Morrissey 1986). The purpose of this study is to examine the concentration of chlorophyll a and c cells as a key to adaptation by corals to photosynthetic irradiance.

Materials and Methods

Twenty pairs of coral tips were cut from representative branches of the upper and lower canopy with bone shears. Ten pairs were analyzed for zooxanthallae per cm2 and ten for chlorophyll concentrations per m2. The same branch cannot be analyxed for both chlorophyll and number of zooxanthallae.

Tips sampled for zooxanthallae were stained with Lugols Iodine Solution and fixed in 10 ml of formalin. Following a 24 h period the excess formalin was drained and replaced with acetic acid for the purpose of decalcification. Every 10-12 h the remaining acid was drained and replaced with fresh solution until all carbonate was dissolved. The flesh was then placed in a tissue grinder to break up the animal tissue for grinding homogenizes single cells for utilization of the hemocytometer.

Tissues being sampled for chlorophyll a and c, were placed in 10 ml of acetone for extraction. Extraction of chlorophyll continued for 24 h in darkness at 4 C. The solution was then centrifuged for a period of one to two minutes in order to settle out any particulate matter. The resulting liquid was transfered to a 1 cm cuvette and placed in the spectrophotometer. Extinction values were measured at 630 nm and 663 nm. Concentrations were calculated from the equations given by Humphrey and Jefferys 1975.

$$\text{Chl a in mg/l} = 11.43\,E_{663} - 0.64\,E_{630}$$
$$\text{Chl c mg/l} = 27.09\,E_{630} - 3.63\,E_{663}$$

Integration was used to calculate surface area. Each branch was considered to be a cylinder and placed on an overhead where the image was projected onto a screen. By placing the tip along side a mm ruler, it was possible to resolve individual mm increments and combine all readings for a final area calculation

$$A_{Total} = h_1d_1 + h_2d_2 + h_3d_3 \ldots h_nd_n$$
$$A = h(d_1 + d_2 + d_3 \ldots)$$

Results

As seen in Table 1, the number of cells found within the canopy of ***P. damicornis*** increases greatly with depth. This is due to the ability of the coral to adapt to solar radiation. Since zooxanthallae harvest sunlight, their numbers, or pigment per cell, must increase in order to maximize photosynthesis in a shaded area. In correlation with the zooxanthallae counts are various concentrations of chlorophyll a and c, resulting from photoadaptation by the colony on the reef flat. Chlorophyll concentration per cell and per unit area increases in the lower canopy (Table 1). This results from a necessity on behalf of ***P. damicornis*** to increase levels of chlorophyll in shade adapted portions to maximize the amount of sunlight captured for photosynthesis. So, concentrations of cells and chlorophyll may increase with depth, but the efficiency or assimilation of the organism decreases with sunlight. Also represented in the table is the amount of chlorophyll per area.

The integrated reef chlorophyll (per m^2 of reef) is four times greater than the total concentration for the ocean station (Table 2). This implies a significant difference in productivity between the two environments. The reasons for this lie in that the reef is a benthic community where there is a high level of nutrient recycled, and the ocean is a biological loss to deep water.. There is very little recycling of nutrients and homogenization of waters. There are no land masses to contribute elements to the water column and when organisms die, they sink to deep depths and decompose below the thermocline, (about 200 m). The temperature differences prevent substantial mixing of waters and consequently the majority of nutrients and chlorophyll remain in deeper zones of the ocean.

Discussion

In 1918 Willstatter and Stoll summarized the results of their studies relating photosynthesis and chlorophyll. They reasoned that photosynthesis might be proportional to the amount of chlorophyll and introduced the concept of assimilation numbers which was defined as the ratio of photosynthetic rate to the weight of chlorophyll (Odum and Odum, 1958). Today, chlorophyll concentrations are used as a measure of overall photosynthetic functions in ecological systems.

In order for coral to harvest the maximum amount of sunlight, coral reefs must adapt to photosynthetic irradiation. As evidenced elsewhere in the paper, whole reef communities rarely receive equal amounts of light saturation. It is therefore noted that inorder to capture maximum light, systems must regulate chlorophyll for maximal photosynthetic production.

Variations in zooxanthallae counts and chlorophyll concentrations in the upper and lower canopy of ***P. damicornis*** suggests photoadaptation on behalf of the colony. However, the effectiveness of adapted chlorophyll for photosynthesis increases with light intensity. Shaded cells of the community possess higher chlorophyll concentrations and lower assimilation numbers (Odum and Odum 1958).

On the other hand, the open ocean, despite its volume is a far less productive environment that the coral reefs. Clear water has a deeper euphotic zone and less chlorophyll per volume. This results from low nutrient levels above the thermocline and poor mixing of the waters.

Summary

1. When examining chlorophyll and zooxanthallae in the reef coral ***P. damicornis,*** it is noted that there is a stratification of both concentrations in response to photoadaptation. The number of cells per area, chlorophyll per cell and per area are increased in the lower canopy, but the efficiency or assimilation of the

organism decreases with sunlight.

2. The the coral reef community contains chlorophyll concentrations four times that of the open ocean per unit area. This implies that the overall productivity of the reef environment is greater than the deep water ocean.

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Table 1. Light effects on zooxathallae (cell) and chlorophyll (chl) distribution in reef coral ***Pocillopora damicornis.*** Pigment area $^{-1}$ = pigment concentration m^2 unit area, pigment cell^{-1} = pigment cell^{-1} concentration mg; cell area = cell density X 10^6 cm^{-2}. Sample size 10 pairs. Values are means ± 1 SD

	Upper canopy	Lower canopy	Sig[a]
Pigment area^{-1}			
chl a	6.44 ± 1.0	1.78 ± 0.54	*
chl c	17.28 ± 3.80	3.90 ± 1.43	*
Pigment cell^{-1}			
chl a	005 ± .30	.01 ± .09	*
chl c	.001 ± .27	.002 ± .10	*
cells area^{-1}	1.2	1.6	

[a] Significance levels as determined from "Crunch": * = p< .0001

Table 2. Mean concentration of chlorophyll a on coral reef vs. GOFS open ocean station mg m^{-2}

Location	Range	Mean
Coral reef	63.44 - 173.17	118.30
GOFS Station	20.5 - 34	30.33
Ratio		1:3.90

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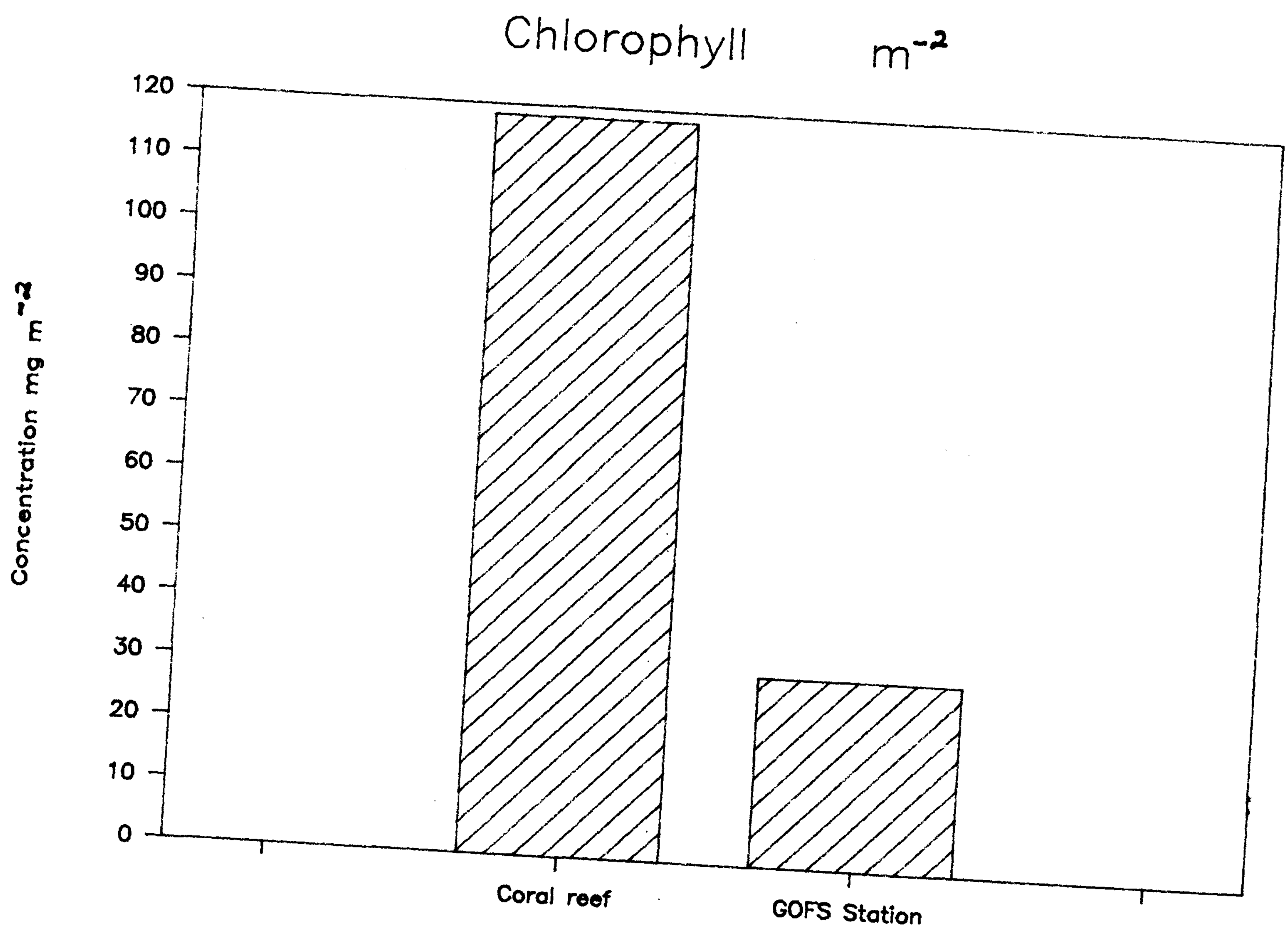
Chlorophyll m-2
Concentration mg m-2
120
110
100
90
80
70
60
50
40
30
20
10
0
Coral reef
GOFS Station

Number of Zooxanthallae